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Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg, 1865 (Onuphidae) in Hawaii: community structure, and sediment stabilizing properties*

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Large numbers of the tube-building polychaete *Diopatra leuckarti* Kinberg form extensive mounds of sand on a Hawaiian reef-flat, providing a stable environment with plentiful resources to support a diverse invertebrate community. The vertically oriented tubes reach densities of 21 800 m^{-2} and the projecting tubes trap drift algae and sediments which are sources of food and tube-building materials for the associated community. There are 22 polychaete species, six crustacean species and eight of other taxa represented, with *Leptochelia dubia* (tanaid) and *Capitella capitata* (capitellid) as the dominant organisms, reaching densities of 32 800 m^{-2} and 11 600 m^{-2}, respectively. Both species form fine mud tubes on the sediment surface among the *Diopatra* tubes. Other numerically abundant taxa are the deposit feeders comprising orbiniid, capitellid and cirratulid polychaetes, small crustaceans and a holothurian. Crustaceans, fishes and polychaetes are the primary predators. Both low salinities (15–26‰ at low tides) due to ground water seepage and fine sediments are probably major factors affecting the species composition of the *Diopatra* mounds. They also act as a buffer between the reef-flat and the beach, serving to reduce beach erosion.

KEY WORDS: Polychaeta – Onuphidae – Hawaii – tube-building – sediment stabilization – faunal communities.

CONTENTS

INTRODUCTION

In this paper I examine some ecological characteristics of a gregarious tube-building species, *Diopatra leuckarti* Kinberg, describing the community associated with this polychaete and its effect on the stability of sediments on a Hawaiian

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reef. Tube-building polychaetes that add sediments to their tubes may occur in dense aggregations and lead to an increase in species richness and diversity (Woodin, 1978; Bailey-Brock, 1979; Wilson, 1979). Such aggregations also stabilize sediments (Fager, 1964; Featherstone & Risk, 1977; Bailey-Brock, 1979), and trap organic materials thereby increasing the amount of food available to deposit feeders (Mangum, Santos & Rhodes, 1968).

The sand-flats of coral reefs have received less attention than sandy shores in temperate latitudes. Extensive inventories of the macrofauna of sand flats on the Australian Barrier Reef, Solomon and Cook Islands have been collated by Gibbs (1971, 1972, 1978). These studies note that gregarious, tube-building polychaetes are conspicuous components of this type of habitat which is characterized by diverse assemblages of invertebrates.

In many coral reef systems, carbonate sediments are transported about the reef and eventually are lost to the deeper offshore waters. Polychaete worms may materially affect the sand budgets of coral reefs. Bailey-Brock (1979) has pointed out the importance of chaetopterids as stabilizers of reef sediments in Hawaii. On south shore Oahu reefs chaetopterids in densities of 11 000 m^{-2} or more, produce raised mounds which comprise different proportions of sediment grain sizes than adjacent areas, and have a characteristic diverse fauna. There are numerous other gregarious tube-building polychaetes present on coral reefs; *Diopatra leuckarti* is one that in dense populations traps fine particles and forms raised mounds adjacent to the beach that may reduce beach erosion and the amount of fines moving on to the reef-flat.

MATERIALS AND METHODS

Study population

The gregarious tube-building onuphid polychaete, *Diopatra leuckarti*, forms mounds in a narrow band adjacent to a sandy beach at Niu Valley on the south shore of Oahu, Hawaii. This polychaete is presently known only from this location in the Hawaiian Islands. The area is fronted by a fringing reef that extends as a shallow reef-flat 700 m from the shoreline and is thus protected from the full force of breaking waves. Onshore and longshore winds disturb surface waters and algal debris is transported on to the beach at high tide. Ground water seepage in the *Diopatra* mounds, visible as small springs, reduces the salinity to 15–26‰ at low tides after periods of heavy rainfall. A nearby channelized stream drains onto the reef-flat at the *Diopatra* beds, and is a source of terrigenous and organic materials. Sediments in the mounds are of carbonate and basalt origin and become black and anoxic 2 cm below the surface.

Tides in Hawaiian waters are semidiurnal, from −10 cm below to +70 cm above chart datum. *Diopatra* mounds are exposed only at tides below 0 to +6 cm, and even then small waves generated by winds may keep the mounds submerged.

Methods

Community sampling

Three replicate samples of sediment-dwelling organisms were taken within 0.25 m distance of each other on 19 January 1979, with a cylindrical corer (1 l capacity, 100 cm^2 surface area). The samples were fixed in 10% formalin, and processed in an acid bath (Brock & Brock, 1977) to remove all carbonate materials. Organisms that remained on the 0.5 mm mesh bottom of the sample containers were then sorted to species under a dissecting microscope. Numbers of individuals and species were computed for species diversity (H'), and proportions of trophic categories in the community.

Sediment sampling

Sediment for grain size analyses was sampled at 2 m intervals along a transect from the upper beach, across the mounds and on to the reef-flat. These samples were wet sieved (Tyler series <0.063–15.85 mm) to separate fractions of different grain sizes, oven dried to a constant weight, and the proportions of grain sizes calculated.

RESULTS

Diopatra leuckarti constructs vertically oriented sand-grain covered tubes up to 7.5 cm long, that project 1–2 cm above the surface of the sediment (Bailey-Brock & Hartman, 1984). Aggregations of the onuphid form extensive mounds 15–20 cm in height, 3–5 m in breadth, and up to 500 m in length, paralleling the shore between the sandy beach and the reef-flat. Densities of these worms may reach 21 800 m^{-2}. The tubes are covered with sand particles, and the portions that project above the mound are bent over in a 'J' shape and ornamented with pieces of algae and vegetation, shell and coral fragments.

The worms are 1.5–3 cm in length, 1.5 mm in width, and remain in the tubes except while feeding when the anterior region (often 1 cm or more) protrudes from the tube mouth to forage in the near vicinity. Worms were observed to feed at low tides when the surface of the mounds and tube openings were fully exposed. They foraged in an arc on the algae attached to neighbouring tubes and on the surface of the sediments. It is not known whether they also feed in a similar fashion at high tides. Feeding in this polychaete family is a controversial subject, but in Hawaii *D. leuckarti* may be eating algae attached to the tubes, and may practise algal gardening as described for other polychaetes (Fauchald & Jumars, 1979). They may also ingest mud, surface-dwelling crustaceans and rafted algae. The most conspicuous algae on the mounds (rafted and attached) are *Acanthophora spicifera*, *Gracilaria bursapastoris*, *Hypnea cervicornis*, *Spiridium filamentosa*, *Padina* spp., *Dictyota acutiloba*, *Lyngbya majuscula*, *Microdictyon setchellianum* and *Ulva fasciata*.

Predation by crustaceans, fish and birds on *Diopatra* was estimated by counting worms with regenerating heads and/or tails. Of the 541 worms in the three samples, 11.8% had regenerating heads and 7.2% had regenerating tails, but this could also be attributed to damage caused by fishermen digging for bait.

The Diopatra community

Specimens collected from three replicate samples are listed in Table 1. Also collected, but not enumerated in Table 1, were unidentified nemerteans and a sponge. The crustaceans, which were almost exclusively the tube dwelling tanaid *Leptochelia dubia*, reached a mean density of 27 700 m^{-2} in the three replicates (Table 1).

Table 1. Numbers of each taxon in three samples from the *Diopatra* mounds. Feeding guilds are included for many components of the community

Taxa	Feeding guilds	x̄(%)	Samples 1	2	3
Polychaeta					
Diopatra leuckarti	BSJO	46.5	218	190	133
Pareurythoe	CMX	8.0	12	0	6
Marphysa macintoshi	CMJ		1	1	0
Dorvillea ?angloana	CMJ		0	4	0
Nematonereis unicornis	CMJ		1	4	1
Lumbrineris heteropoda	CMJ		6	1	9
L. dentata	CMJ		0	1	0
Nereis arenaceodonta	CMJ		5	9	1
Sphaerosyllis sp.	CMJ		8	6	9
Typosyllis sp. A	CMJ		2	3	1
Typosyllis sp. B	CMJ		2	0	0
Exogone verugera	HMJ	13.3	51	25	79
Naineris laevigata	BMX	24.3	1	2	1
Scoloplella sp.	BMX		1	0	0
Dasybranchus lumbricoides	BMX		0	4	0
Capitella capitata	BMX		116	59	99
Cirratulus zebuensis	SDT	7.8	3	1	4
Cirriformia punctata	SDT		1	2	1
Cirriformia sp.	SDT		44	10	20
Polydora pilikia	F–SDT		1	3	0
P. armata	F–SDT		0	0	1
Total Polychaeta			473	325	365
Crustacea					
Leptochelia dubia	DP		260	171	280
Gammarid sp.	DP		0	6	9
Tanaid sp.	DP		31	32	39
Copepod	F–DP		1	0	0
Penaeid	DP		1	0	0
Crab	C		1	0	0
Total Crustacea			294	209	328
Gastropoda			1	6	0
Nematoda			79	38	73
Sipuncula					
Aspidosiphonidae	F–DP		1	1	2
Sipunculan	F–DP		1	1	1
Anthozoa					
Anemone	C		0	1	0
Palythoa vestitus	DP–A		6	5	5
Holothuroidea					
Holothuria parvula	DP		1	0	0
Total number of species			28	26	21
Total number of individuals			856	586	774
Community diversity (H′)*			1.86	1.84	1.82
Polychaete diversity (H′)			1.58	1.48	1.61

*Nematodes and sponges omitted.

Polychaete feeding guilds abbreviations: BSJO, burrowing, sessile, jawed, omnivore; HMJ, herbivore, motile, jawed; SDT, surface deposit feeding, discretely motile, tentaculate; CMJ, carnivore, motile, jawed; BMX, burrowing, motile non-jawed; F–SDT, filtering and surface deposit feeding. Feeding guilds abbreviations for other taxa: DP, deposit feeding; F–DP, filtering and deposit feeding; C, carnivore; A, autotroph.

Cirratulids and capitellids were most numerous polychaetes, especially *Capitella capitata*. The orbiniid, *Naineris laevigata*, is a large worm that forms deep burrows in the mounds and may not have been sampled adequately with 10 cm deep cores. Oxygenated sediments (pale in colour) were seen along the edges of the burrow within the anoxic layer indicating that the burrowing activities of this worm aid in percolation of oxygen within the mound. The spionids, *Polydora armata* and *P. pilikia* are both coral borers (Ward, 1981) and were probably living withing small pieces of coral rubble. The reef-inhabiting opheliid *Armandia intermedia* was not taken in quantitative samples, but is frequently found among the *Diopatra* tubes. It is a surface sediment dweller that is often taken in plankton tows and is eaten by fishes, especially members of the family Mullidae (Sorden, 1983). The common reef-flat zoanthid, *Palythoa vestitus*, a solitary form that attaches to pieces of coral rubble which serve as subsurface anchors within the mounds, may assist in stabilizing sediments. When conditions of low water motion prevail the oral disc is fully expanded to 10 mm diameter.

The polychaetes associated with *Diopatra* have been assigned to feeding guilds (Fauchald & Jumars, 1979) which reflect motility, procurement, and type of food eaten by these worms (Table 1). *Capitella capitata,* which is considered to be a burrowing, motile, non-jawed form that also forms tubes of sediment, was included with the other burrowing deposit feeders. Of the six feeding guilds represented by the 21 polychaete species, only one species (*D. leuckarti* itself) represented burrowing, sessile, jawed omnivores and comprised 46% of all polychaetes from the three samples (Table 1). In all three replicates the burrowing, deposit feeding category (capitellids and orbiniids) ranked second with 24%, and the motile, jawed herbivore (*Exogone verugera*) ranked third at 13% of all polychaetes collected. Jawed carnivores and filtering and tentaculate surface deposit feeding forms were poorly represented in these samples (Table 1). When proportions of deposit feeders were calculated for the entire community (omitting nematodes), 55.5% were found to feed on detritus. Some use sediment to form tubes, e.g. *Capitella capitata* and *Leptochelia dubia* (tanaid), thus contributing to the retention and packing of materials in the mounds. The burrowers are essentially bioturbators, mixing and loosening some of the sediment by burrowing, which aids the percolation of water and oxygen within and below the mound.

Sediment distribution

Mound sediments comprise materials that originate on the reef (carbonate particles and deteriorating algae) and on land (vegetation and basaltic materials), and that vary in diameter from pebbles (15 mm or more) to muds which are dark in colour, indicating a high organic content, probably from all the particulate plant material. Beach sediments also originate from the same sources but are light in colour and probably of a lower organic content as they contain less particulate plant material. Grain sizes of 0.5–1 mm predominate on the beach (Fig. 1), with a predominance of fine particles (80° are < 0.5 mm) at the top of the beach, becoming coarser (almost 90% are 0.5–1 or 2 mm) towards and seaward end. A trough at the junction of the beach and the mounds contained large pieces of coral rubble. Three replicates from the mounds showed the predominance of fine particles, almost 90% are < 0.5 mm flat from the beach. Water movement is slowed at the mounds, and this buffering effect must help to reduce beach erosion and cause deposition of fine particles on the mounds. Almost 40° of the mound sediment was < 0.063 mm, while less than 7% of this size fraction was found on the reef a few metres seaward. Only the most shoreward chaetopterid mound sample had 10% of the < 0.063 mm fraction. The other stations had considerably less fine material both within and adjacent to the mounds. The rubble (15 mm diameter and larger) remains in the trough (Fig. 1) and causes scouring of the trough walls during normal water movement.

Diopatra mounds provide a nutritionally rich system. Projecting ends of tubes catch sediments and drift algae which are sources of food and cover for many components of the community. Herbivores and detritivores have a ready food supply and gain protection from predators and desiccation while feeding during low tides. The packing of sediments provides substratum stability for tube dwellers and burrowers, and the high organic content of the trapped material serves as a food source for selective and burrowing detritivores. Consequently a community has developed around the *Diopatra* tubes taking advantage of these resources. Some species are surface sediment dwellers that form temporary, fine mud tubes (*Leptochelia dubia,* tanaid; *Capitella capitata,* capitellid) and are deposit feeders (Table 1). Others are burrowers, motile or sedentary, jawed or jawless forms, that feed as omnivores and deposit feeders. Only one species, *Exogone verugera* (syllid) can be classed as a jawed herbivore, while many species are motile carnivores (e.g. syllids, nereids, eunicids and lumbrinerids). The selective, deposit-feeding spionids, *Polydora armata* and *P. pilikia,* are not sediment dwelling species and were no doubt present in small pieces of coral rubble at the surface of the mound. The stomatopod (*Pseudosquilla ciliata*), orbiniid (*Naineris laevigata*), capitellid (*Dasybranchus lumbricoides*), cirratulids and holothurian (*Holothuria parvula*) form burrows. The polychaetes *Capitella capitata, Pareurythoe* sp., all syllids and the crustaceans *Leptochelia dubia,* the gammarid and another tanaid species are sediment surface dwellers. *Leptochelia dubia* does not tolerate smothering by even small amounts of sediment and will vacate the tubes to avoid suspended material (Brenchley, 1981). Both the capitellid and tanaid benefit from the stable food-rich habitat that exists among the *Diopatra* tubes and in turn their presence may help to stabilize mound sediments.

A number of predaceous species live in the *Diopatra* mound habitat. Nemerteans, hermit crabs (*Calcinus laevimanus*), calappid crabs (*Calappa hepatica*), mantis shrimps (*Pseudosquilla ciliata*) and a number of small fishes (*Bathygobius* sp., juvenile *Mulloidichtys* spp., *Kuhlia sandvicensis* and *Asterropteryx semipunctatus*) may all prey on *Diopatra* and other taxa in the community. *Nothria holobranchiata* was a major component of the gut contents of mullids in the Northwestern Hawaiian Islands (Sorden, 1983). Shore birds including *Pluvialis dominica,* an omnivore, occasionally feed on the exposed mounds at low tide; prey items are predominately crustaceans, melanid snails and plant materials (Okimoto, 1975).

The main forces of disturbance in this habitat are the burrowing activities of calappid crabs which do not have permanent burrows, and fishermen digging for bait. The influence of the latter is probably the most detrimental on these communities as it brings deep anoxic sediments to the surface, buries surface sediment, creates steep sided holes that cause the sediments and worm tubes to wash out, and results in the removal of the orbiniid (used as bait). The effects of man's disturbance have not been measured or addressed in this study, but the mounds eventually reform and regain much of their former elevation with time.

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REFERENCES

BAILEY-BROCK, J. H., 1979. Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. *Journal of Marine Research, 37:* 643–656.

BAILEY-BROCK, J. H. & HARTMAN, O., 1984. Polychaeta (Annelida) of the Hawaiian Islands. Revision of *Reef and Shore Fauna of Hawaii* by C. H. Edmondson. Bishop Museum Press (in press).

BRENCHLEY, G. A., 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *Journal of Marine Research, 39:* 767–790.

BROCK, R. E. & BROCK, J. H., 1977. A method for quantitatively assessing the infaunal community in coral rock. *Limnology and Oceanography, 22:* 948–951.

FAGER, E. W., 1964. Marine sediments: Effects of a tube-building polychaete. *Science, 143:* 356–359.

FAUCHALD, K. & JUMARS, P. A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology, Annual Review, 17:* 193–284.

FEATHERSTONE, R. P. & RISK, M. J., 1977. Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology, 47:* 446–450.

GIBBS, P. E., 1971. The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History) Zoology, 21:* 101–211.

GIBBS, P. E., 1972. Polychaete annelids from the Cook Islands. *Journal of Zoology, London, 168:* 199–220.

GIBBS, P. E., 1978. Macrofauna of the intertidal sand flats on low wooded islands, northern Great Barrier Reef. *Philosophical Transactions of the Royal Society of London B 284:* 81–97.

MANGUM, C., SANTOS, S. & RHODES, W., JR, 1968. Distribution and feeding in the onuphid polychaete, *Diopatra cuprea* Bosc. *Marine Biology, 2:* 33–40.

OKIMOTO, B. F., 1975. *Parasites of the Golden Plover and their use as biological markers.* Masters Thesis. University of Hawaii.

SORDEN, C., 1983. *Trophic relationships of Goatfishes (Family Mullidae) in the Northwestern Hawaiian Islands.* Masters Thesis. University of Hawaii.

WARD, L. A., 1981. Spionidae (Polychaeta: Annelida) from Hawaii with descriptions of five new species. *Proceedings of the Biological Soceity of Washington, 94:* 713–730.

WILSON, H. W., 1979. Community structure and species diversity of the sedimentary reefs constructed by *Petaloproctus socialis* (Polychaeta: Maldanidae). *Journal of Marine Research, 37:* 623–641.

WOODIN, S. A., 1978. Refuges, disturbance and community structure: a marine soft-bottom example. *Ecology, 59:* 274–284.